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COMPARATIVE OSTEOLOGY OF THE SUSPENSORIAL COMPLEX OF ALGAL-FEEDING CICHLIDS (PISCES, TELEOSTEI) FROM LAKE TANGANYIKA

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ABSTRACT The comparative osteology of the suspensorial complex in 20 species of epilithic algal feeders from Lake Tanganyika was studied as a means of obtaining fundamental data for understanding the adaptive radiation in feeding habits of cichlid fishes in the East African lakes. Six types of suspensorial complex could be recognized within the 20 species studied. For the palatine, ectopterygoid, entopterygoid, metapterygoid, quadrate, symplectic, preoperculum and hyomandibula, 5, 2, 3, 3, 5, 2, 2 and 5 types were recognizable respectively. The relation between the morphology of the suspensorial complex and feeding habits is discussed.

Key Words: Lake Tanganyika; Cichlidae; Algal feeder; Suspensorial complex: Comparative morphology.

INTRODUCTION

Cichlids in Lake Tanganyika represent the most outstanding example of adaptive radiation with respect to feeding habits among three great lakes in East Africa: Victoria, Malawi and Tanganyika (Fryer & Iles, 1972). Since morphological features especially related to feeding are supposed to exhibit a higher degree of diversification, Tanganyika cichlids could be an ideal fish group to study the relation between morphology and ecology. However, there has been no comprehensive osteological work, except Mbomba (1983) and Yamaoka (1988) on the jaws of epilithic algal feeders. In the present study, I describe the morphology of the suspensorial complex in 20 species as a part of the comparative osteology of the syncranium of epilithic algal-feeding cichlids.

MATERIALS AND METHODS

The 12 genera and 20 species studied are listed below. The range of standard lengths in mm and sample sizes are shown in parentheses: *Asprotilapia leptura* Boulenger (14.6–89.5 mm, 5 specimens), *Cyathopharynx furcifer* (Boulenger) (9.2–139.4, 5), *Eretmodus cyanostictus* Boulenger (7.6–62.3, 7), *Limnotilapia dardennei* (Boulenger) (25.2–142.3, 5), *L. loocki* Poll (37.6–121.4, 4), *Ophthalmotilapia nasuta* (Poll & Matthes) (22.3–134.0, 6), *Petrochromis polyodon* Boulenger (10.6–165.3, 17), *P. fasciolatus* Boulenger (12.3–116.8, 13), *P. trewavasae* Poll (33.0–160.4, 14), *P. orthognathus* Matthes (16 7–140.4, 12), *P. famula* Matthes & Trewavas (17.2–114.2, 12),

P. macrognathus Yamaoka (56.5–172.2, 4), *Pseudosimochromis curvifrons* Poll (14.3–89.4, 7), *Simochromis diagramma* Günther (11.0–132.5, 11), *S. babaulti* Pellegrin (8.4–64.8, 8), *S. marginatus* Poll (15.7–79.7, 9), *Spathodus marlieri* Poll (42.4–63.0, 3), *Tanganicodus irsacae* Poll (6.9–55.0, 6), *Telmatochromis temporalis* Boulenger (11.5–63.7, 7), *Tropheus moorei* Boulenger (5.8–98.7, 10).

Material was mostly collected from October 1979 through February 1980 and from August through December 1981, mainly on the northwestern rocky shore near Luhanga (3°31'S, 29°09'E). All specimens of *Limnotilapia loocki*, however, were collected at Kigoma on the east coast in 1983.

All laboratory observations and drawings were made with the aid of Wild-M7S stereoscopic dissecting microscope and camera lucida. Skeletons were stained with alizarin red S after the fleshy parts were removed with KOH solution. Glycerol was used as a clearing agent. The osteological nomenclatures mainly follow Barel et al. (1976). The suspensorial complex includes the suspensorium and palatopterygoid arch.

RESULTS

The suspensorium and palatopterygoid arch are a rather plate-like complex, situated just ventral to the orbit, the latter forming a lateral wall to the oral cavity. The complex plays an important role as the main site of origin for the adductor mandibulae muscles. It has, roughly speaking, a quadrangular shape. Both its dorsorostral and dorsocaudal ends articulate movably with the neurocranium. Furthermore, its ventrorostral end has a synovial joint with the lower jaw. The suspensorial complex consists of 8 components: palatine, ectopterygoid, entopterygoid, metapterygoid,

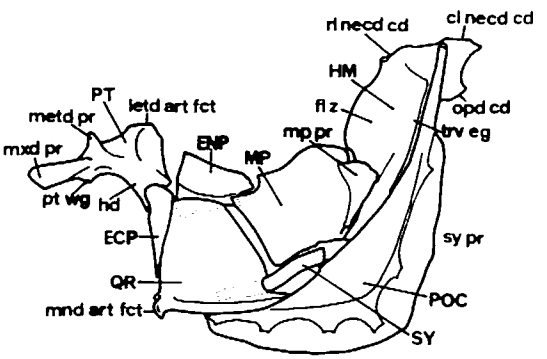

Fig. 1. Lateral view of the suspensorium of a specimen, 50.6 mm SL, of *Limnotilapia loocki*. ECP: Ectopterygoid; ENP: Entopterygoid; HM: Hyomandibula; MP: Metapterygoid; POC: Preopercular; PT: Palatine; QR: Quadrate; SY: Symplectic; cl necd cd: caudal neurocraniad condyle; fl z: flange zone; hd: handle; letd art fct: lateroethmoidad articulation facet; metd pr: mesethmoidad process; mnd art fact: mandibulad articulation facet; mp pr: metaperygoid process; mxd pr: maxillad process; opd cd: operculad condyle; pt wg: palatine wing; rl necd cd: rostral neurocraniad condyle; sy pr: symplectic process; trv eg: transverse edge. Scale = 5 mm.

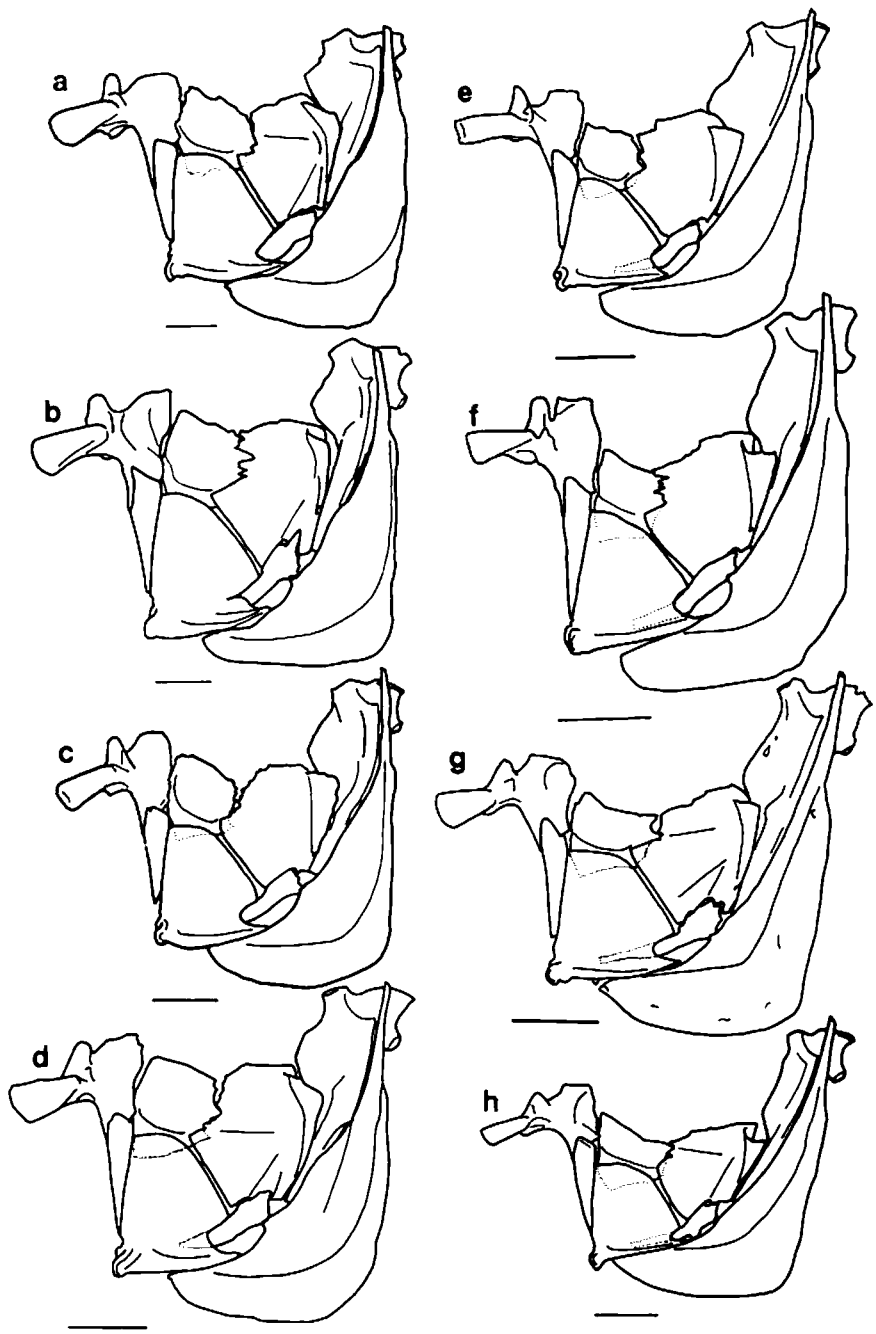

Fig. 2. Lateral view of the suspensorium. a) *Petrochromis macrognathus*, 172.2 mm SL, b) *P. polyodon*, 165.3 mm SL, c) *P. trewavasae*, 130.3 mm SL, d) *P. famula*, 114.2 mm SL, e) *P. orthognathus*, 114.3 mm SL, f) *P. fasciolatus*, 115.0 mm SL, g) *Limnotilapia loocki*, 121.4 mm SL, h) *L. dardennei*, 142.3 mm SL. Scale = 5 mm.

quadrate, symplectic, hyomandibula and preoperculum (Fig. 1). Since the complex has a plate-like, relatively solid structure, I think it better first to treat it as one unit before considering the individual elements.

Based on the overall morphology of the adult suspensorial complex, the apparatus of 20 species can be grouped into 6 types.

Petrochromis type (Fig. 2): *Petrochromis* spp. and *Limnotilapia* spp. (8 spp.) share the following features: 1) The ventrorostral margin of the complex at the ectopterygoid and quadrate runs almost vertically and is parallel to the caudal margin of the vertical limb of the preoperculum, 2) the maxillad process of the palatine is moderate in both stoutness and length, and its mesethmoidad process and lateroethmoidad articulation facet are situated well dorsad, 3) the depth of the suspensorial complex at the level of the metapterygoid is not shallow, but rather deep. 4) the relation between the palatine and entopterygoid is intimate (the bones tend to be connected weakly in some species), 5) the depression between the rostral and caudal neurocraniad condyles of the hyomandibula is shallow, and 6) the dorsal tip of the preoperculum extends beyond the dorsal margin of the hyomandibula.

Among the 8 species having this type of complex, *P. macrognathus*, *P. polyodon*, *P. trewavasae* and *P. famula* have a deepest suspensorial complex at the level of the metapterygoid.

Simochromis type (Fig. 3): *Simochromis* spp., *Pseudosimochromis curvifrons* and *Tropheus moorei* (5 spp.) seem to share some features with those in the Petrochromis type. However, these 5 species have the following characteristic features: 1) The whole rostral part of the complex protrudes rostrad, and as a result its ventrorostral margin (mainly at the ectopterygoid) has a weak rostrad inclination and is not parallel to the caudal margin of the preoperculum. 2) The dorsal tip of the preoperculum extends beyond the dorsal margin of the hyomandibula or is at nearly the same level.

Eretmodus type (Fig. 4): *E. cyanostictus*, *Spathodus marlieri* and *Tanganicodus irsacae* share some features with those of the Petrochromis type. However, these three species differ in having the dorsal tip of the preoperculum lower than the dorsal margin of the hyomandibula.

Asprotilapia type (Fig. 5): *A. leptura* has the following unique features: 1) The palatine is much enlarged, protruding well rostrad, the maxillad process elongate but the mesethmoidad process weakly developed, 2) the ventrorostral margin of the suspensorial complex is inclined weakly rostrad, and not parallel to the caudal margin of the preoperculum, 3) although the palatine is distinctly separated from the entopterygoid, the gap is rather narrow and the dorsal end of the latter bone is clearly at more dorsal level than the caudoventral end of the former bone, 4) the depth of the suspensorial complex at the level of the metapterygoid is rather shallow, 5) the dorsal end of the preoperculum lies above the dorsal margin of the hyomandibula, and 6) the depression between the rostral and caudal neurocraniad condyles of the hyomandibula is very shallow.

Cyathopharynx type (Fig. 6): *C. furcifer* and *Ophthalmotilapia nasuta* share some features with *A. leptura*. However, these two species differ from that type in the follow-

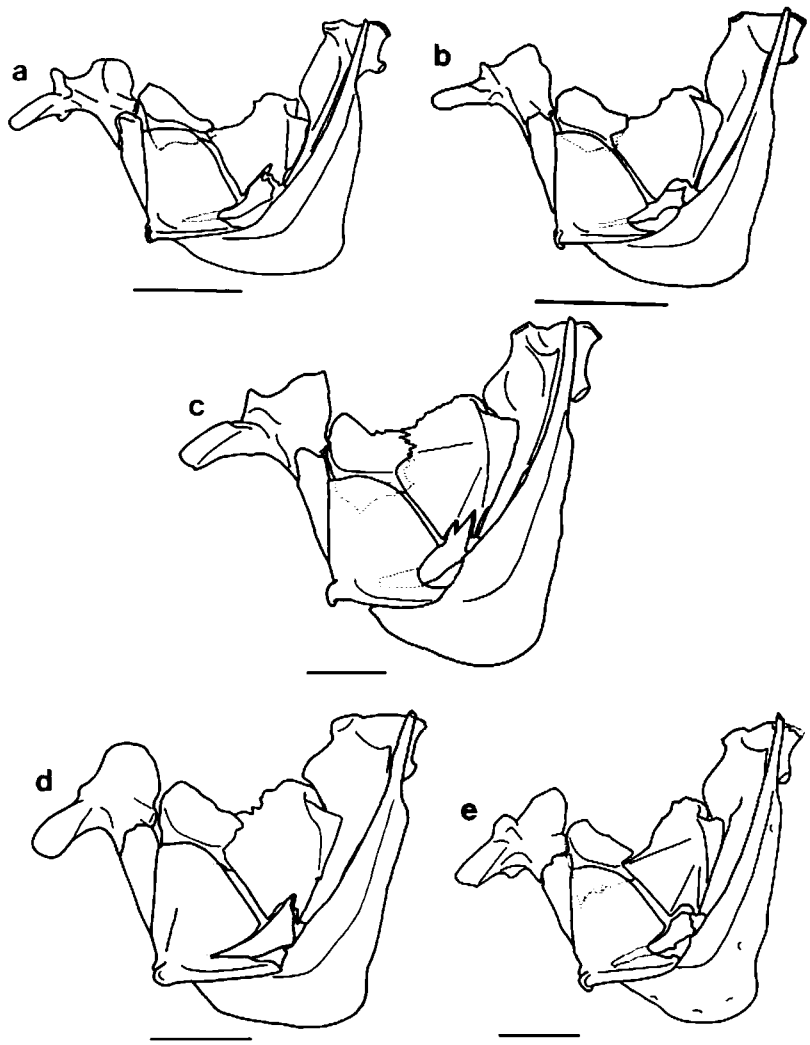

Fig. 3. Lateral view of the suspensorium. a) *Simochromis marginatus*, 74.8 mm SL, b) *S. babaulti*, 64.8 mm SL, c) *S. diagramma*, 132.5 mm SL, d) *Pseudosimochromis curvifrons*, 89.4 mm SL, e) *Tropheus moorei*, 98.7 mm SL. Scale = 5 mm.

ing features: 1) Although the palatine is large, its maxillad process is not elongate, 2) the gap between the palatine and entopterygoid is wide and the dorsal end of the latter bone does not extend dorsad above the level of the caudoventral end of the former bone, 3) the depth of the suspensorial complex at the level of the metapterygoid is distinctly shallow, and the eye border is deeper, and 4) since the rostral neurocraniad condyle of the hyomandibula projects considerably dorsorostrad, the depression between two condyles is greater.

Telmatochromis type (Fig. 7): *T. temporalis* has the following unique features: 1)

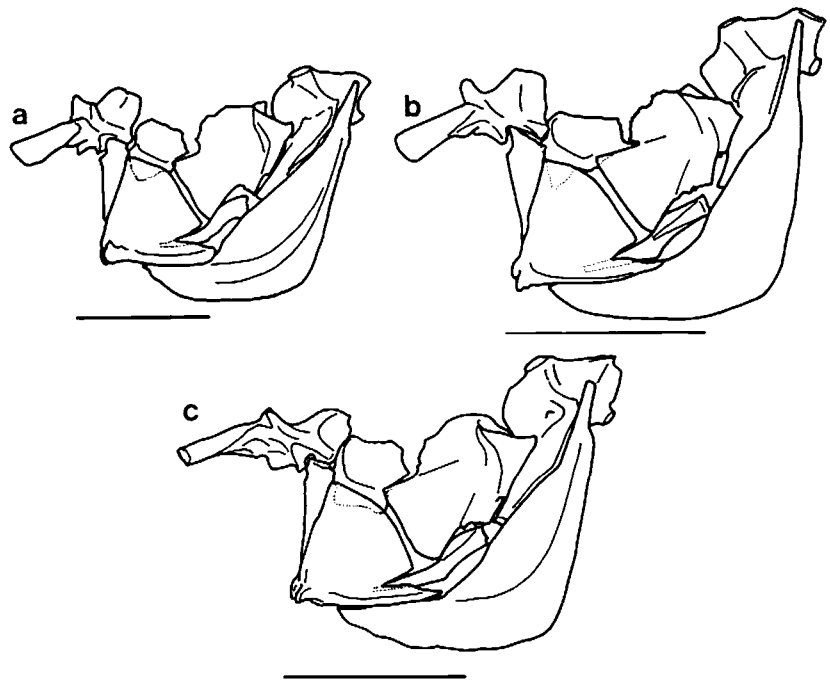

Fig. 4. Lateral view of the suspensorium. a) *Eretmodus cyanostictus*, 62.3 mm SL, b) *Spathodus marlieri*, 50.1 mm SL, c) *Tanganicodus irsacae*, 55.0 mm SL. Scale = 5 mm.

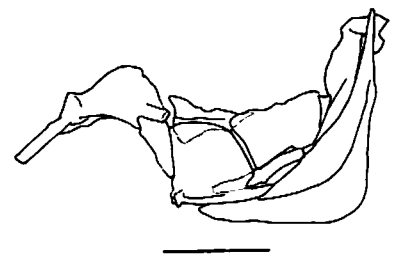

Fig. 5. Lateral view of the suspensorium of a specimen, 89.5 mm SL, of *Asprotilapia leptura*. Scale = 5 mm.

The palatine is broad, especially at its caudoventral region and, as a whole, protrudes considerably rostrad, 2) the lateroethmoidad articulation facet of the palatine is not markedly expanded dorsad and its dorsal end lies at a lower level than that of the mesethmoidad process, which projects markedly dorsad, 3) the sutural junction between the palantine and ectopterygoid is large, 4) the relation between the palatine and entopterygoid is intimate, 5) the depression between the rostral and caudal neurocraniad condyles of the hyomandibula is conspicuously deep because of a rostrodorsad projection of the rostral neurocraniad condyle, 6) the dorsal end of the

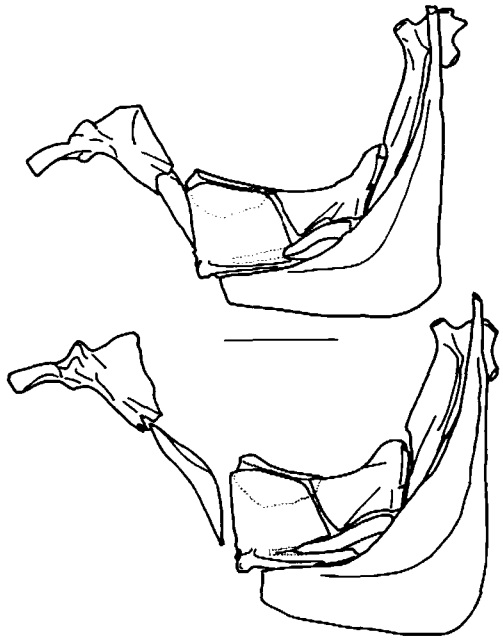

Fig. 6. Lateral view of the suspensorium. Upper, *Cyathopharynx furcifer*, 89.0 mm SL; lower, *Ophthalmotilapia nasuta*, 134.0 mm SL. Articulations at the palatine region are separated in lower figure. Scale = 5 mm.

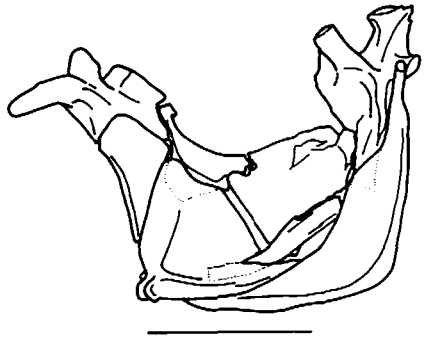

Fig. 7. Lateral view of the suspensorium of a specimen, 62.0 mm SL, of *Telmatochromis temporalis*. Scale = 5 mm.

preoperculum is noticeably lower than the dorsal margin of the hyomandibula, 7) the ventrorostral margin of the suspensorial complex at the ectopterygoid is inclined weakly rostrad, and 8) origins of the adductor mandibulae muscles tend to be lengthened and caudally ends reach almost the caudal margin of the vertical limb of the preoperculum.

In smaller specimens of all species examined, the connections between the elements

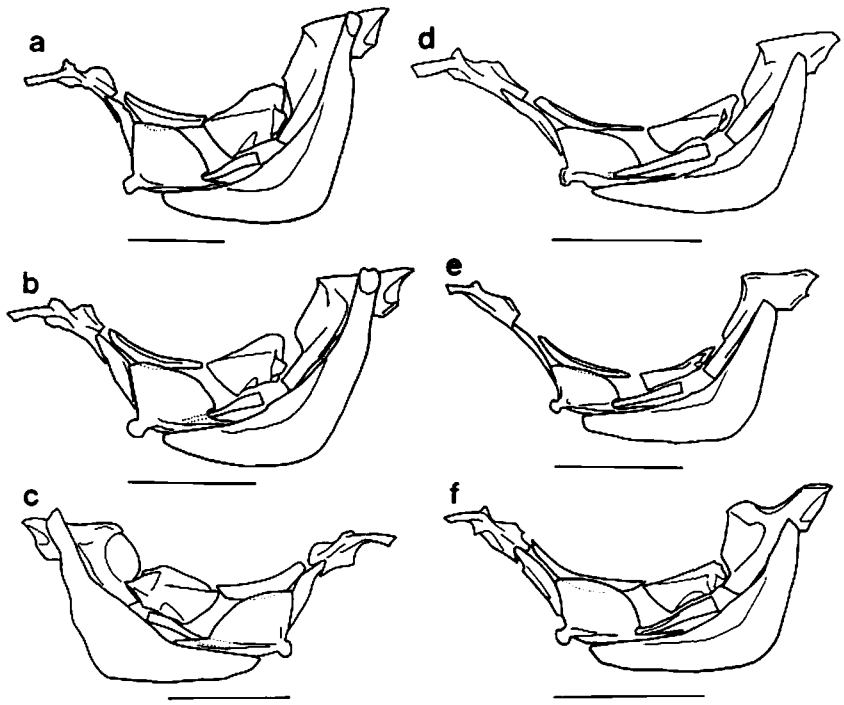

Fig. 8. Lateral view of the suspensorium. a) *Petrochromis orthognathus*, 16.7 mm SL, b) *Simochromis marginatus*, 15.7 mm SL, c) *Eretmodus cyanastictus*, 14.1 mm SL, d) *Asprotilapia leptura*, 14.6 mm SL, e) *Cyathopharynx furcifer*, 13.4 mm SL, f) *Telmatochromis temporalis*, 11.5 mm SL. Scale = 1 mm.

of the suspensorial complex are weak and, as a whole it is shallower, especially at the level of the metapterygoid (Fig. 8). The ventrorostral margin mainly at the ectopterygoid inclines further rostrad than in larger specimens. The dorsal end of the palatine appears to be at lower level when compared with that of the hyomandibula in larger specimens.

Components of the Suspensorial Complex

Palatine

This component is a pistol-shaped bone, lying at the rostrodorsal end of the complex. It consists of two areas; the rostral maxillad process and the caudal handle (Fig. 1). The maxillad process extends rostrad or ventrorostrad and its distal end rests on the palatinad wing of the maxilla. The handle is provided with three projections (Fig. 1). Two of them are at the dorsal and ventral margins just caudal to the maxillad process. The former is the mesethmoidad process, the latter the palatine wing, which in its position resembles the trigger of a pistol. The third projection is a large one, lying dorsocaudal to the mesethmoidad process, and is called the lateroethmoidad articulation facet. The cudoventral region extends ventrad to articulate mainly with

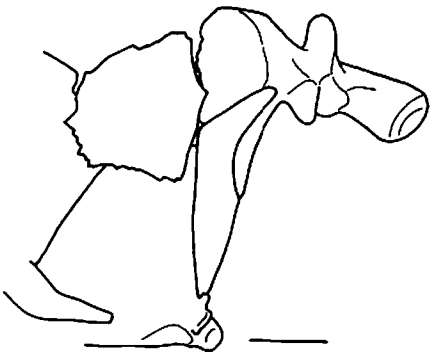

Fig. 9. Medial view of the palatine region of a specimen, 172.2 mm SL, of *Petrochromis macrognathus*. Scale = 5 mm.

the ectopterygoid by a notch (Fig. 9). Although the degree of intimacy of contact between the palatine and entopterygoid varies interspecifically, these two bones are not inflexibly articulated with each other. The medial face of the palatine wing is tightly bound to the lateral face of the former.

Five types of the palatine are recognized in the adult stage based not only on the shape of the bone but also on its relative position and on its relation to other bony elements.

Petrochromis type (Figs. 2, 3): *Petrochromis* spp., *Simochromis* spp., *Pseudosimochromis curvifrons*, *Tropheus moorei* and *Limnotilapia* spp. (13 spp.) share the following features: 1) The maxillad process is moderately or very short and generally extends ventrorostrad, 2) the lateroethmoidad articulation facet is well developed and its dorsal end reaches a level above or almost equal to that of the mesethmoidad process, 3) the caudoventral region extends considerably ventrad or at least perceptibly so, 4) the articulation between the palatine and ectopterygoid is not weak, and 5) the relation between the palatine and entopterygoid is intimate.

Among 13 species, there are considerable interspecific variations in palatine shape. In *P. fasciolatus* and *P. orthognathus*, the maxillad process extends slightly rostrad rather than ventrorostrad (Fig. 2). A depression between the mesethmoidad process and the lateroethmoidad articulation facet in *P. fasciolatus* is uniquely narrow and deep (Fig. 2). In *L. dardennei*, the dorsal end of the palatine seems to be at lower level than that of the hyomandibula in the other 12 species (Fig. 2). In *Tropheus moorei* and *Pseudosimochromis curvifrons*, the lateroethmoidad articulation facet is well expanded dorsad and the maxillad process is stout and short (Fig. 3). The caudoventral region does not extend far ventrad in these two species.

Eretmodus type (Fig. 4): *E. cyanostictus*, *S. marlieri* and *T. irsacae* share the following features: 1) The maxillad process is rather long, 2) the caudoventral region extends only slightly ventrad, and 3) the connection between the palatine and ectopterygoid seems to be feeble because only small part of the ectopterygoid is covered by the palatine.

Other features are similar to those of the Petrochromis type.
Asprotilapia type (Fig. 5): *A. leptura* has the following features: 1) The maxillad process is somewhat slenderly elongate and extending well ventrorostrad, 2) the lateroethmoidad articulation facet is broad and its dorsal end extends further dorsad than that of the mesethmoidad process, 3) the articulation between the palatine and ectopterygoid seems to be strong, 4) the caudoventral region extends considerably caudoventrad, and 5) the palatine is clearly separated from the entopterygoid.
Cyathopharynx type (Fig. 6): *C. furcifer* and *O. nasuta* share the following features: 1) The maxillad process is rather short and slender, 2) the caudoventral region extends well caudoventrad, 3) the articulation between the palatine and ectopterygoid seems to be strong, and 4) the palatine is widely separated from the entopterygoid.
Telmatochromis type (Fig. 7): *T. temporalis* has the following features: 1) The maxillad process is short and markedly stout, 2) the lateroethmoidad articulation facet is not well developed and its dorsal end is at a lower level than that of the mesethmoidad process which extends well dorsad, 3) the caudoventral region is wide and extends considerably ventrad, 4) the connecting line between the palatine and ectopterygoid is long and the articulation between them does not seem to be weak, and 5) the relation between the palatine and entopterygoid is intimate and a small concavity is developed at the ventrocaudal corner of the palatine to receive the dorsal end of the entopterygoid.

In smaller specimens examined, the lateroethmoidad articulation facet is weakly developed and its dorsal end is either at a lower level than or is almost equal to that of the mesethmoidad process (Fig. 8).

Ectopterygoid

The component is, in general, an elongate triangular bone of which base faces rostrad (Fig. 9). It lies between the palatine and quadrate and forms a ventrorostral margin of the suspensorial complex.

Two types of the ectopterygoid are recognized in the adult stage.

Petrochromis type (Fig. 9): All species in the present study except *Telmatochromis temporalis* share the following features that the ectopterygoid is, roughly speaking, a triangular or falciform and narrow bone.

Among the 19 species, the bone in *Tropheus moorei* and *Pseudosimochromis curvifrons* tends to be a little wider.
Telmatochromis type (Fig. 10): *T. temporalis* has the unique features that the bone shows a somewhat quadrangle rather than triangle and it is much widened.

The ectopterygoid becomes wider with growth in all species studied.

Entopterygoid

The component is a plate-like bone which forms a part of the eye border. It is

surrounded rostrally by the palatine and ectopterygoid, ventrally by the quadrate and caudally by the metapterygoid (Fig. 1). When it is articulated with other bones, it is covered by them.

Three types of the entopterygoid can be recognized in the adult stage.

Petrochromis type (Figs. 2–4): *Petrochromis* spp., *Limnotilapia* spp., *Simochromis* spp., *Pseudosimochromis curvifrons*, *Tropheus moorei*, *Eretmodus cyanostictus*, *Spathodus marlieri* and *Tanganicodus irsacae* (16 spp.) all share the feature of the entopterygoid tending to be quadrangular in shape.

Among these 16 species, the bone of *Petrochromis* spp. and *T. moorei* is greater in its relative depth, especially in *P. polyodon*, *P. trewavasae*, *P. macrognathus* and *P. famula* (Fig. 2). In these 4 species, the dorsal end of the entopterygoid reaches dorsally to a point near that of the lateroethmoidad articulation facet of the palatine. In *E. cyanostictus*, *S. marlieri* and *T. irsacae*, the bone seems to be relatively small (Fig. 4).

Cyathopharynx type (Figs. 5, 6): In *Cyathopharynx furcifer*, *Ophthalmotilapia nasuta* and *Asprotilapia leptura* the entopterygoid is rather reduced in depth and its caudal end tends to taper gradually.

Telmatochromis type (Fig. 7): *T. temporalis* has the unique features of the entopterygoid being relatively shallower, its rostrodorsal end extends well dorsad and is slender.

In smaller specimens of all species examined, the entopterygoid is a slender, crescent-shaped bone and increases in depth with growth (Fig. 8).

Metapterygoid

This component is a plate-like bone with a flap-like metapterygoid process at its caudal end (Fig. 1). Its dorsal margin forms a part of the eye border. It is surrounded rostrally by the entopterygoid and quadrate, ventrally by the symplectic and caudally by the hyomandibula. The connections between these bones are mainly cartilaginous.

Three types of the metapterygoid are recognized in the adult stage.

Petrochromis type (Figs. 2–4): *Petrochromis* spp., *Limnotilapia* spp., *Simochromis* spp., *Pseudosimochromis curvifrons*, *Tropheus moorei*, *Eretmodus cyanostictus*, *Spathodus marlieri* and *Tanganicodus irsacae* (16 spp.) share the following features: 1) The

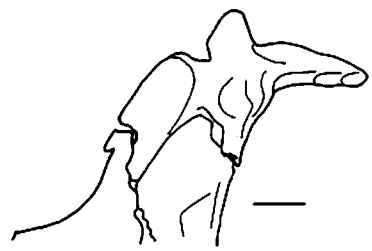

Fig. 10. Medial view of the rostrodorsal region of a specimen, 62.0 mm SL, of *Telmatochromis temporalis*. Scale = 1 mm.

bone is not quadrangular in shape and its caudodorsal part is expanded dorsad and 2) the metapterygoid process is large.

Among the 16 species, the bone of *Petrochromis* spp., *Limnotilapia loocki*, *Tropheus moorei*, *Simochromis diagramma* and *Pseudosimochromis curvifrons* tends to be relatively deeper.

Cyathopharynx type (Figs. 5, 6): *Cyathopharynx furcifer*, *Ophthalmotilapia nasuta* and *Asprotilapia leptura* share the following features: 1) The bone has, roughly speaking, an elongate quadrangular shape and is shallow and 2) the metapterygoid process is small.

Among these three species, the bone of *C. furcifer* and *O. nasuta* extends considerably caudodorsad but does not do so in *A. leptura*.

Telmatochromis type (Fig. 7): *T. temporalis* has the following features: 1) The bone has an elongate quadrangular shape and 2) the metapterygoid process is small and another flap is developed rostral to it.

In smaller specimens of all species examined, the metapterygoid tends to be a shallow elongate quadrangular bone (Fig. 8). It increases in depth with growth. The bone in the adult specimen of *L. dardennei* is somewhat similar in shape to that of other species in smaller specimens of the Petrochromis type.

Quadrate

This component is a round, fan-shaped bone, occupying the rostroventral part of the suspensorial complex (Fig. 1). The mandibulad articulation facet, forming a stout synovial joint with the articular is developed at its rostral-ventral corner. A caudal process and notch are visible ventrocaudally and the symplectic inserts into the medial face of the latter (Fig. 1). The quadrate is surrounded by, rostrally, the ectopterygoid, dorsally the entopterygoid, caudally by the metapterygoid and symplectic, and ventrally by the preoperculum. The connection with the metapterygoid is by cartilaginous tissue.

Five types of the quadrate are recognized in the adult stage.

Simochromis type (Figs. 2, 3): *Petrochromis polyodon*, *P. trewavasae*, *P. famula*, *P. macrognathus*, *Simochromis* spp., *Tropheus moorei*, *Pseudosimochromis curvifrons* and *Limnotilapia* spp. (11 spp.) share the following features: 1) The depth of the quadrate is greater than its length, 2) the rostral and ventral margins make nearly a right or slightly smaller angle with each other, and 3) the caudal process does not extend far caudad.

Among the 11 species, *L. dardennei* tends to have a smaller notch.

Fasciolatus type (Fig. 2): *Petrochromis fasciolatus* and *P. orthognathus* have a quadrate similar to that of the Simochromis type. However, the bone in two species differs from the Simochromis type in the following points: 1) Its depth is almost equal to its length and 2) the angle between the rostral and ventral margins is less than 90°.

Eretmodus type (Fig. 4): *Eretmodus cyanostictus*, *Spathodus marlieri* and *Tanganicodus irsacae* share the following features: 1) The length is greater than the depth, 2)

the angle between the rostral and ventral margins is distinctly smaller than 90°, and 3) the caudal process generally extends well caudad and the notch tends to be narrow and deep.

Cyathopharynx type (Figs. 5, 6): *Cyathopharynx furcifer*, *Ophthalmotilapia nasuta* and *Asprotilapia leptura* share the following features: 1) The length is larger than the height, 2) the rostral and ventral margins make just a right angle with each other, and 3) the caudal process extends caudad well.

Among the three species, the dorsal margin of *A. leptura* is considerably expanded.

Telmatochromis type (Fig. 7): *T. temporalis* has the following features: 1) The length is larger than the depth, 2) the caudal process extends well caudad and the notch is moderate in size, 3) the rostrodorsal corner of the bone tends to be round, not angular, and 4) the angle between the rostral and ventral margins is less than 90°.

In smaller specimens of all species examined, the quadrate is rather a shallow bone and it increases in depth with growth (Fig. 8). The caudal process is slenderly developed caudad and the notch is smaller than that of in adult specimens. The angle between the rostral and ventral margins becomes smaller with growth.

Symplectic

This component of the complex is an elongate, plate-like bone, lying between the ventral end of the hyomandibula and quadrate (Fig. 1). Its rostral half inserts into the medial face of the quadrate. The bone generally becomes gradually more slender rostrad. The caudal end is connected to the ventral end of the hyomandibula through cartilaginous tissue. It is surrounded by, dorsally, the metapterygoid and, ventrally, by the preoperculum.

Two types of the symplectic are recognized in the adult stage.

Petrochromis type (Figs. 2–4, 6): *Petrochromis* spp., *Limnotilapia* spp., *Simochromis* spp., *Pseudosimochromis curvifrons*, *Tropheus moorei*, *Eretmodus cyanostictus*, *Spathodus marlieri*, *Tanganicodus irsacae*, *Cyathopharynx furcifer* and *Ophthalmotilapia nasuta* (18 spp.) have the caudal part of the bone widest.

Among these 18 species, the caudal part of the bone in *C. furcifer* and *O. nasuta* tends to be narrower than those in the other species.

Telmatochromis type (Figs. 5, 7): *Telmatochromis temporalis* and *Asprotilapia leptura* share the feature that the bone is widest at its middle part and not the caudal part.

In smaller specimens examined, the symplectic is more straight and slender a bone than that of adults and it is only slightly widened caudad in all species, including *T. temporalis* and *A. leptura* (Fig. 8).

Preoperculum

The preoperculum is a boomerang-shaped and large bone, which forms the ventral

and caudal margins of the suspensorial complex (Fig. 1). There are 7 openings to the lateral-line system.

Two types of the preoperculum seem to be recognized in the adult stage.

Petrochromis type (Figs. 2–6): All species in the present study except *T. temporalis* share the following features: 1) The vertical limb is longer than the horizontal limb and 2) the limbs make a right or larger angle with each other.

Among the 19 species, the horizontal limb of *Petrochromis* spp., *Limnotilapia* spp., *Simochromis* spp., *Pseudosimochromis curvifrons* and *Tropheus moorei* (13 spp.) is conspicuously shorter than the vertical limb. By contrast, the horizontal limb of *Eretmodus cyanostictus*, *Spathodus marlieri*, *Tanganicodus irsacae* and *Asprotilapia leptura* is relatively lengthened and is only a little shorter than the vertical one. The vertical and horizontal limbs of *Petrochromis macrognathus*, *P. polyodon*, *P. trewavasae*, *P. famula*, *Cyathopharynx furcifer* and *Ophthalmotilapia nasuta* make almost a right angle with each other.

Telmatochromis type (Fig. 7): *T. temporalis* is unique in the 20 species in having vertical and horizontal limbs of nearly equal length. They make an angle larger than 90° with each other.

In smaller specimens of all species examined, the horizontal limb is relatively longer than those in larger specimens. The angle between the two limbs seems to become slightly smaller with growth (Fig. 8).

Hyomandibula

This component is a solid and rugged bone of complex shape which connects the caudodorsal part of the suspensorial complex with the brain case and the operculum (Fig. 1). It has three condyles, of which the rostral and dorsal ones have synovial joint with the neurocranium and the caudal one articulates with the hyomandibulad socket of the operculum. The rostral margin of the bone just ventral to the rostral neurocraniad condyle forms the caudal part of the eye border. A wide hyomandibular flange zone is developed caudal to the rostral margin, and at its caudodorsal end is produced into the hyomandibular transverse edge. A symplectic process (arm) is also developed.

Five types of the hyomandibula are recognized in the adult stage.

Petrochromis type (Figs. 2, 3): *Petrochromis* spp., *Simochromis* spp., *Limnotilapia loocki*, *Pseudosimochromis curvifrons* and *Tropheus moorei* (12 spp.) share the following features: 1) The depression between the rostral and dorsal neurocraniad condyles is, if present, shallow, 2) the hyomandibular flange zone is not so expanded dorsoventrad and as a result its rostral margin is not so long, and 3) the symplectic process is noticeably long.

P. macrognathus and *P. polyodon* in particular have a short rostral margin and, by contrast, *L. loocki* has a somewhat long one.

Asprotilapia type (Fig. 5): *Asprotilapia leptura* and *Limnotilapia dardennei* have a similar hyomandibula to that of the Petrochromis type. However, it differs in that the bone itself is slender and its rostral margin tends to be elongate.
Eretmodus type (Fig. 4): *Eretmodus cyanostictus*, *Spathodus marlieri* and *Tanganicodus irsacae* share the following features: 1) The depression between the rostral and dorsal neurocraniad condyles is wide and shallow, 2) the hyomandibula itself is shortened in depth, and its rostral margin is short and is expanded rostrad, and 3) the symplectic process is rather short.
Cyathopharynx type (Fig. 6): *Cyathopharynx furcifer* and *Ophthalmotilapia nasuta* share the following features: 1) The depression between the rostral and dorsal neurocraniad condyles seems to be a little deeper than that in the previous three types and 2) the hyomandibula itself is very slender and its rostral margin is greatly elongate.
The symplectic process of *O. nasuta* seems to be shorter than that of *C. furcifer*.
Telmatochromis type (Fig. 7): *T. temporalis* is very distinctive in that the rostral and caudal neurocraniad condyles project distinctly and the depression between them is prominently deepened. The symplectic process is stout and short, and the hyomandibular flange zone is small.

In smaller specimens of all species examined, the symplectic process is short and becomes longer with growth (Fig. 8). Two neurocraniad condyles are not projected at all and are inconspicuous in lateral view. The shallow depression is discernible only in *T. temporalis*. Generally, the dorsal end of the hyomandibula extends well caudodorsad.

DISCUSSION

The following three regions or features of the suspensorial complex can be suggested as having adaptive significance: the palatine region; the hyomandibula; and the depth of the complex at the level of the metapterygoid (Fig. 1). These parameters are generally closely correlated with the characteristic feeding behaviour, and the morphology of the palatine region is especially distinctive in relation to the feeding behaviour.
Asprotilapia leptura, *Cyathopharynx furcifer* and *Ophthalmotilapia nasuta* (Figs. 5, 6), tappers or suckers (Yamaoka, pers. obs.), which have been treated as members of the *Ophthalmotilapia* assemblage (Greenwood, 1983), have in common the following morphological features, as partly suggested by Liem (1981). i) The palatine projects well rostrad and the palatopterygoid gap is clearly discernible. ii) The vertical depth of the complex at the level of the metapterygoid is shallow. iii) The hyomandibula itself is a slender, elongate bone and its rostral and caudal neurocraniad condyles are slightly separated from each other.
All these features can be related with the weaker biting force and friction of the jaws against rocky substrata. Liem (1981) reported that the functional significance of the obvious separation of the entopterygoid from the palatine remains unclear because no correlation between this specialized feature and specializations in other morphological and functional features could be recognized. However, it may at least be re-

marked that the presence of a distinct gap means a weakening of the suspensorial complex in the palatine and pterygoid region. Since the abduction of the complex seriously affecting the upper jaw movement (Alexander, 1967) cannot be transmitted directly to the palatine because of the unrigidness of the region, the controlling ability of the maxillad process of the palatine over the articulation head of the maxilla seems to be decreased. This supposition is supported by the fact that the three species, when feeding, do not press the jaws strongly and intimately against the rocky substrata (Yamaoka, pers. obs.). Though Liem & Osse (1875) pointed out that taxa with great mobility of the upper jaw possess a relatively small palatine bone which is joined to the ectopterygoid only, *A. leptura*, which has great upper jaw mobility, has an enlarged palatine (Fig. 5). This contradiction remains to be answered.

Since a large part of the lateral face of the suspensorial complex serves as a site of origin for the adductor mandibulae muscles, shallowness in the region necessarily means that the muscles are less voluminous. The decreased muscles indicate a smaller biting force.

Liem (1981) reported that the hyomandibula of *Asprotilapia* and *Ophthalmotilapia* is slender with an elongate symplectic process. However, Greenwood (1983), on the basis of extensive outgroup comparisons, rejected Liem's (1981) view and concluded that the symplectic process of *Asprotilapia*, *Ophthalmotilapia* and *Cyathopharynx* is no longer than that in generalized species or that of other Tanganyika genera. In the present study, the symplectic process of the three genera is not so elongate, which leads me to agree with Greenwood (1983).

Liem & Osse (1975) reported that in gape-and-suck feeders, the hyomandibula is a slender bone with slightly separated neurocraniad condyles. Therefore, their narrow separation seems to be related with sucking. In fact, *A. leptura*, *C. furcifer* and *O. nasuta* appear to adopt a sucking mode of feeding (Yamaoka, pers. obs.).

The remaining 17 epilithic algal feeders are alike in showing the following features. The palatine region is shortened and the entopterygoid is attached to the caudal margin of the palatine as in generalized cichlids (Liem & Osse, 1975; Barel et al., 1976), or the two elements abut against each other (Figs. 2, 3). The depth of the suspensorial complex at the level of the metapterygoid is large. The hyomandibula is generally broadened and the two neurocraniad condyles are rather widely separated.

These features may be related with the strong biting force and hard friction of the jaws against rock surface inferred from the followings. Taxa with trophic adaptations requiring strength and stability of the upper jaw have a large palatine connected to both the ectopterygoid and entopterygoid (Liem & Osse, 1975). The deep lateral face of the suspensorial complex plays a role of an increased site of origin for the voluminous adductor mandibulae muscles (Barel, 1985) supposedly contributing to the strong biting force (Barel, 1983). As for the hyomandibula, Liem & Osse (1975) also reported that many algal feeders show a trend toward a very broad hyomandibula with widely separated neurocraniad condyles.

There is some small variation in morphological features within the 17 species I have examined. The relation between the palatine and pterygoid region in *Telmatochromis temporalis* si most intimate, though the palatine region has a considerably rostrad

projection. The neurocraniad condyles in the species are very widely separated by a distinct concavity, and the hyomandibula itself is broadened with a short symplectic process. According to Liem & Osse (1975), the symplectic process is shortened in algal feeders. These features are in accord with the fact that *T. temporalis* seemingly has a unique browsing behaviour which requires hard biting (Yamaoka, 1983b).

The considerable rostrad projection of the palatine region, and the intimate relation between the palatine and ptergoid region (Fig. 3) found in the browsers, *Tropheus*, *Pseudosimochromis* and *Simochromis*, may be interpreted as follows. The rostrad projection of the palatine region is associated with rather the ventral position of the mouth in these species (Regan, 1920; Brichard, 1978). This suggestion is supported by the fact that *L. dardennei*, despite it being a browser, has a terminal, rather small mouth (Regan, 1920) and the palatine region itself does not project so far rostrad.

Grazers have following features in common. The palatine region does not project so far rostrad as it does in most browsing species (Fig. 2) and the vertical depth of the suspensorial complex at the level of the metapterygoid is greater than in browsers.

In *Petrochromis* spp., the rostrad projection of the palatine and the direction of the maxillad process of that bone seem to be related to the degree to which the upper jaw can be projected rostrad. *P. macrognathus*, having the most projecting upper jaw (Yamaoka, 1983a), shows the most projecting palatine region, and its relatively stout maxillad process does not extend rostrad but weakly ventrorostrad (Fig. 2). In contrast, *P. fasciolatus*, which alone among *Petrochromis* spp. has a prognathous lower jaw (Poll, 1956; Brichard, 1978; Yamaoka, 1983a), does not show a rostrad projection of the palatine region, and its relatively slender maxillad process tends to extend rostrad (Fig. 2). Though the remaining 4 congeners show an intermediate condition of these features, *P. orthognathus*, however, has a relatively slender maxillad process which extends rostrad (Fig. 2), and thus approaches the condition in *P. fasciolatus*. These two species also have a shallower vertical depth at the level of the metapterygoid than do the other 4 congeners (Fig. 2) which have been regarded as highly specialized grazing species (Yamaoka, 1982, 1983a, 1983b). In addition, *P. fasciolatus* and *P. orthognathus* have a more slender and narrower flange zone than do other members of the genus. *Limnotilapia loocki* has similar morphological features to those of *P. orthognathus* (Fig. 2): both species have isognathous jaws (Yamaoka, 1983a; see Poll, 1956). Since these three species are categorized as a group with a lower degree of adaptation to grazing (Yamaoka, 1982, 1983b; Hori & Kuwamura, pers. comm.), the common occurrence amongst them of a relatively slender maxillad process, a shallow depth at the metapterygoid level, and a slender and narrow flange zone of the hyomandibula are associated with the weaker biting forces produced by these species when grazing. On the other hand, the features found in *P. macrognathus*, *P. polyodon*, *P. trewavasae* and *P. famula* can probably be looked upon as adaptations producing stronger biting forces.

Interspecific differences in the degree of rostrad projection of the palatine region are correlated with the angle between the rostral and ventral margins of the quadrate in grazers. Species with nearly a right angle between those margins, that is, with the rostral margin almost perpendicular to the longitudinal body axis (Fig. 2), have a

rostrad projecting palatine region. In contrast, species with a smaller angle between the two margins do not have such a rostrad projecting palatine region (Fig. 2).

The suspensorial complex of *Limnotilapia dardennei*, as a whole, is similar to that of *L. loocki*. However, *L. dardennei*, a browser, is unique in having a more elongate hyomandibula with a slender flange zone and weakly separated neurocraniad condyles like that of *Asprotilapia leptura*, and a slightly smaller depth at the metapterygoid level than in *L. loocki*. These unique features in a browser are explained in connection with its habit toward omnivory (Hori et al., 1983; Takamura, 1984) and its distributional and behavioural features (Kawabata & Mihigo, 1982; Yamaoka, 1983b). These suggest that the feeding behaviour of *L. dardennei* has been retained at the level of that in its ancestral form and that sucking may considerably take part in its browsing behaviour.

Concerning *Eretmodus cyanostictus*, *Spathodus marlieri* and *Tanganicodus irsacae*, though Liem (1979) pointed out that the ectopterygoid of *Spathodus* and *Tanganicodus* is vertical and has a straight rostral margin and, in contrast, in *Eretmodus* the rostral edge is concave and the bone is obliquely positioned, such interspecific difference in those foregoing features of the palatine region were not found among them in the present study. However, these three species did show interspecific morphological variation in the stoutness of the maxillad process of the palatine, with *T. irsacae* having a rather slender process (Fig. 4) and *E. cyanostictus* and *S. marlieri* a somewhat stout one. This morphological difference is related to differences in feeding behaviour: *T. iresaca* is a picker and the other two species are scrapers (Yamaoka et al., 1986). Picking is supposed to place a smaller burden on the jaws than does scraping, and could thus account for the variation in the stoutness of the palatine.

The hyomandibula of the three species shows a similar pattern to that of *T. temporalis* (Fig. 7). A broad and short hyomandibula with a short symplectic process decreasing the degree and velocity of suspensorial abduction but increasing the space for the adductor mandibulae muscle complex, is found in many epitlithic algal feeders (Liem & Osse, 1975). Therefore, this hyomandibular feature, together with the large depth at the matapterygoid level, shows that the morphology of the suspensorial complex in the three species can be interpreted as an adaptation for feeding on epilithic algae. If that is true, the trend toward insectivory shown by *T. irsacae* (Yamaoka et al., 1986) must be recognized as a secondary specialization, at least as inferred from the morphology of the suspensorial complex.

The morphological features in smaller specimens of the 20 species discussed above are similar to those in adult specimens of *A. leptura*, *C. furcifer* and *O. nasuta* (Fig. 8) which appear to employ sucking behaviour when feeding (Yamaoka, pers. obs.). Therefore, smaller specimens can be assumed to feed by sucking. This assumption is supported by Liem (1980) who suggests that in their ontogeny all cichlids pass through a stage during which they exclusively take food by means of slow, horizontal inertial sucking.

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